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Resurrection and distribution extension of *Odorrana heatwolei* (Stuart & Bain, 2005) (Anura, Ranidae)

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Abstract

We collected nine specimens of *Odorrana* Fei, Ye & Huang, 1990 from Xishuangbanna Prefecture, Yunnan Province, China, which is close to the type locality of *O. heatwolei* (Stuart & Bain, 2005) in Phongsaly Province, northern Laos (approximately 60 km). These specimens agree with the diagnosis of *O. heatwolei* that body size is large in females and relatively small in males, tympanum large in males and relatively small in females, first finger longer than the second, and glandular dorsolateral fold and external vocal sacs present in males, moreover, these specimens have obvious dense tiny black dots scattered on the dorsum, which is consistent with the characters of *O. heatwolei* and different from *O. tiannanensis* (Yang & Li, 1980). Phylogenetically, the sequences of these specimens clustered with the sequence of the holotype of *O. heatwolei* and formed a distinct clade together, which is sister to *O. tiannanensis*. We resurrect *O. heatwolei* and extend the distribution of this species to China.

Key Words

16S rRNA, China, Laos, new record, revalidation, taxonomy

Introduction

The odorous frogs of the genus *Odorrana* Fei, Ye & Huang, 1990 comprise a species-rich group of ranids whose range covers the Ryukyu Archipelago, southern China, northeastern India, and Indochina, and extend southwards to Sumatra and Borneo (Frost 2023). This genus contains 62 recognized species to date, more than half of which occur in southern China (AmphibiaChina 2023; Frost 2023).

Odorrana tiannanensis (Yang & Li, 1980), a species of *Odorrana*, was considered to be widely distributed in southern Yunnan, China, and northern Vietnam and northern Laos (Yang and Li 1980; Yang and Rao 2008; AmphibiaChina 2023; Frost 2023), and its type locality is in Hekou County, Yunnan Province, China (Yang and Li 1980). *Rana heatwolei* Stuart & Bain, 2005 is a species described from Phongsaly Province, northern Laos, and was placed into synonymy of *O. tiannanensis* based on morphological characteristics by Ohler (2007). Poyarkov et al. (2021) regarded it as *O. heatwolei* (Stuart & Bain, 2005) and considered it to be a valid species but did not provide any evidence.

During our field surveys in southern Yunnan Province, China, from 2019 to 2021, we collected 11 specimens of *Odorrana tiannanensis* from its type locality Hekou County, and from Gejiu City and Malipo County, and nine specimens of *O.* cf. *tiannanensis* from Mengla County, which is close to Phongsaly, the type locality of *O. heatwolei* in northern Laos (Fig. 1).

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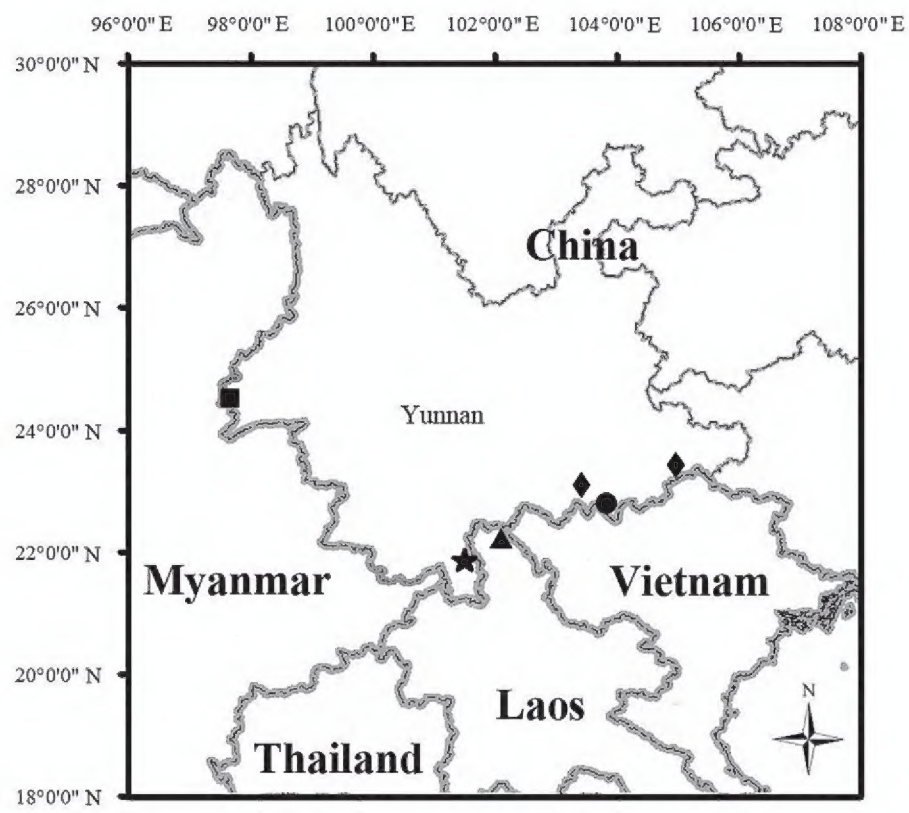

Figure 1. Map showing the type locality (black dot) of *O. tiannanensis*, the type locality (black triangle) of *O. heatwolei*, the type locality (black square) of *O. macrotympana*, the new collection site (black star) of *O. heatwolei*, and the new collection sites (black diamonds) of *O. tiannanensis*.

Molecularly, the sequences of these specimens from Mengla clustered with the sequence of the holotype (FMNH 258134) of *O. heatwolei* and the sequences which were also collected from Phongsaly but identified as *O. tiannanensis* from GenBank, and together, they formed a distinct clade sister to *O. tiannanensis*. The morphological characters of the specimens from Mengla agree with the original description (Stuart and Bain 2005) of *O. heatwolei* but differ from *O. tiannanensis*.

Herein, we resurrect *Odorrana heatwolei* and first report this species from China.

Materials and methods

Taxon sampling

Specimens were euthanised and fixed in 75% ethanol for storage. Liver tissue samples were preserved in 99% ethanol for molecular analysis. All specimens were deposited at Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ).

Molecular analysis

Total genomic DNA was extracted from liver tissues of the specimens from Yunnan, China. A fragment of the mitochondrial 16S rRNA gene was amplified via the polymerase chain reaction (PCR) using the primers L2188 (Matsui et al. 2006): 5'–AAAGTGGGCCTAAAAGCAGCCA–3' and 16H1 (Hedges 1994): 5'–CTCCGGTCTGAACTCAGATCACGTAGG–3'. Molecular experiment protocols used in this study were the same as those in Liu et al. (2022). The sequence of the holotype (FMNH 258134) of *Odorrana heatwolei* was provided by Dr. Bryan L. Stuart from North Carolina Museum of Natural Sciences, all new sequences have been deposited on GenBank, and other sequences were downloaded from GenBank (Table 1). Sequences of *Rana chensinensis* David, 1875 and *Pelophylax nigromaculatus* (Hallowell, 1861) were used as outgroups (Chen et al. 2013; Liu et al. 2021). The technical computation methods for the sequence alignment, genetic divergences calculation, best substitution model selection, Bayesian inference and Maximum likelihood phylogenetic analyses were the same as those in Liu et al. (2022).

Morphology

Measurements were taken with a digital caliper to the nearest 0.1 mm. Combining Liu et al. (2021), Luo et al. (2021), and Liu et al. (2022), we measured: eye diameter (ED), diameter of exposed portion of eyeball; finger disk width (FDW3), width at the widest part of the disk of finger III; forearm and hand length (FHL), from elbow to tip of finger III; foot length (FTL), from the base of inner metatarsal tubercle to the tip of fourth toe; internarial distance (IND), minimum distance between the inner margins of the external nares; interorbital distance (IOD), minimum distance between the inner edges of the upper eyelids; hand length (HAL), from the base of the thenar tubercle to the tip of finger III; head length (HL), from tip of snout to rear of jaw; head width (HW), width of head at widest point; total leg length (LEG), from vent to tip of toe IV; snout length (SL), distance from the tip of the snout to the anterior corner of the eye; snout-vent length (SVL), from tip of snout to vent; tympanum diameter (TD), maximum diameter of tympanum; tympanum-eye distance (TED), from anterior edge of tympanum to posterior corner of the eye; tarsus and foot length (TFL), from heel to the tip of toe IV; tibia length (TL), distance from knee to heel; and upper eyelid width (UEW), maximum width of the upper eyelids.

Results

The sequence alignment is 1090 bp in length. The Maximum likelihood and Bayesian inference phylogenetic trees were essentially consistent. The sequences of the specimens from Mengla, Yunnan, China, the sequence of the holotype (FMNH 258134) of *Odorrana heatwolei*, and the sequences identified as *O. tiannanensis* from Phongsaly, Laos, clustered together, and they formed a distinct clade sister to *O. tiannanensis* with strong supports (Bayesian posterior probability 1, Maximum likelihood bootstrap support 98) (Fig. 2). The genetic divergence (uncorrected p-distance) between the sequences of the specimens from Mengla and the sequence of the holotype (FMNH 258134) of *O. heatwolei* was 0.20%,

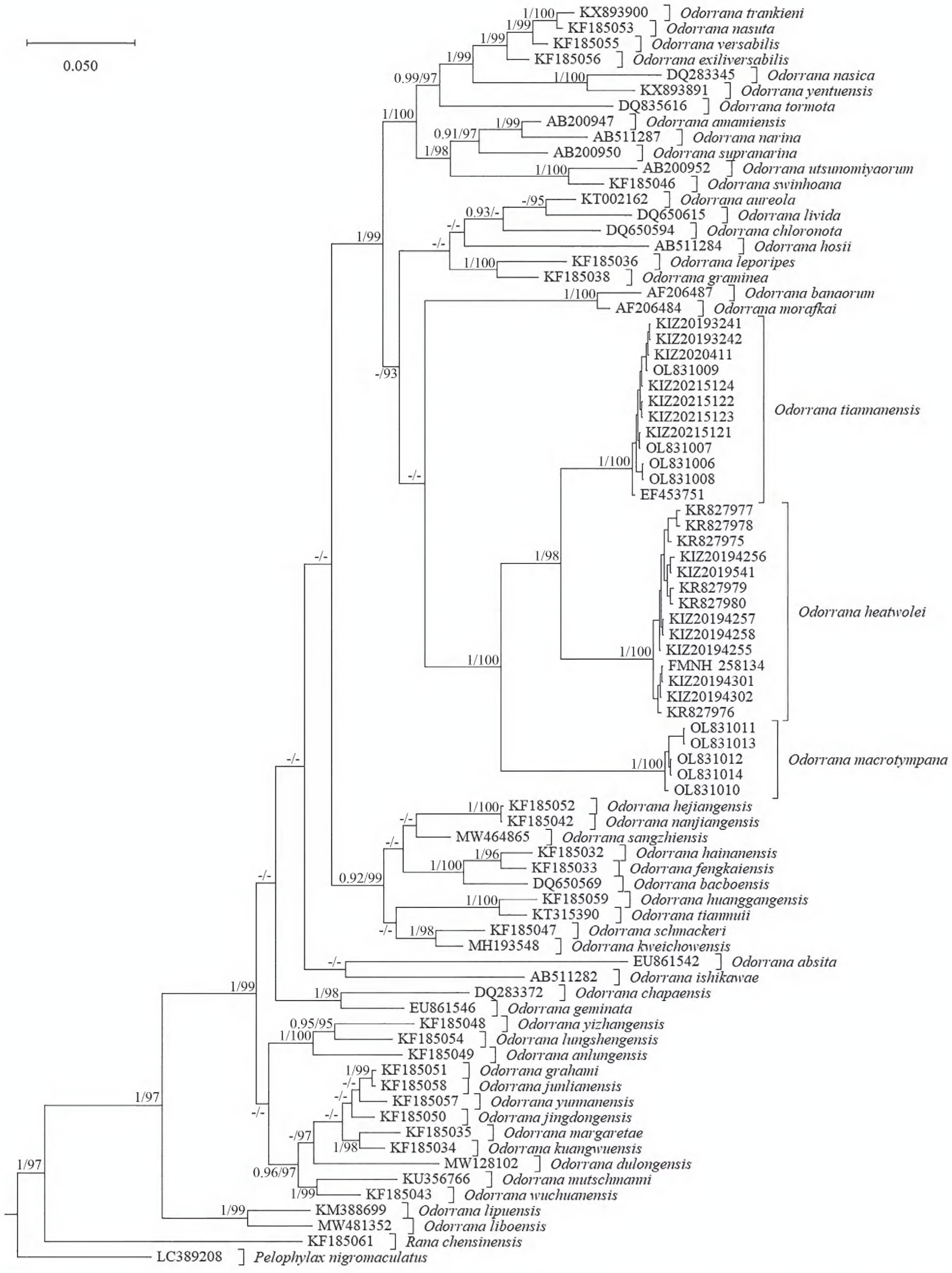

Figure 2. Bayesian inference tree of the genus *Odorrana* based on the mitochondrial 16S rRNA sequences. Numbers before slashes indicate Bayesian posterior probabilities (≥ 0.90) and numbers after slashes indicate bootstrap supports from Maximum likelihood analysis (≥ 90).

between the sequences identified as *O. tiannanensis* from Phongsaly and the sequence of the holotype (FMNH 258134) of *O. heatwolei* was 0.28%, between the sequences of the specimens from Mengla and the sequences of *O. tiannanensis* was 6.51%, and between the sequence of the holotype (FMNH 258134) of *O. heatwolei* and the sequences of *O. tiannanensis* was 6.47% (Table 2).

Morphologically, the specimens from Mengla differ from *Odorrana tiannanensis* by having obvious dense tiny black dots scattered on dorsum and lacking large black dots on dorsum (Figs 3A, C, 4) whereas having distinct or indistinct large black dots on dorsum and lacking dense tiny black dots scattered on dorsum in *O. tiannanensis* (Figs 3B, D, 5). However, morphological characters of the specimens from Mengla are similar to the original description and pictures of *O. heatwolei* in Stuart and Bain (2005).

Therefore, we consider the specimens from Mengla to be *Odorrana heatwolei* which were originally described as *Rana heatwolei* by Stuart and Bain (2005). We formally remove *O. heatwolei* from the synonymy of *O. tiannanensis*.

Taxonomy

Odorrana heatwolei (Stuart & Bain, 2005)

Figs 3A, C, 4, 6, 7

Rana heatwolei Stuart & Bain, 2005

Rana tiannanensis – Ohler, 2007

Odorrana heatwolei – Poyarkov et al., 2021

Type material. ***Holotype*:** FMNH 258134, adult male.

Paratypes. FMNH 258279–83, 258598, six females; FMNH 258135–39, five males.

Type locality. Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos (22°05'38"N, 102°12'50"E; alt. 600 m).

Etymology. The specific epithet is a patronym for Dr. Harold F. Heatwole. We propose "Dense-spotted Odorous Frog" for the English name and "麻点臭蛙" (má diǎn chòu wā) for the Chinese name.

Updated diagnosis. Habitus robust; body sizes of females approximately two to three times that of males,

Table 1. Samples used for phylogenetic analyses of molecular sequence data. * = type locality.

Species	Locality	Voucher NO.	GenBank NO.
Odorrana absita	Xe Sap, Xe Kong, Laos*	FMNH258109	EU861542
Odorrana amamiensis	Tokunoshima, Ryukyu, Japan	KUHE24635	AB200947
Odorrana anlungensis	Anlong, Guizhou, China*	HNNU1008I109	KF185049
Odorrana aureola	Phu Luang, Loei, Thailand*	ZMKU AM 01137	KT002162
Odorrana bacboensis	Khe Moi, Nghe An, Vietnam*	FMNH255611	DQ650569
Odorrana banaorum	Tram Lap, Gia Lai, Vietnam	ROM7472	AF206487
Odorrana chapaensis	Lai Chau, Vietnam	AMNH A161439	DQ283372
Odorrana chloronota	Darjeeling, West Bengal, India*	BMNH 1947.2.28.6	DQ650594
Odorrana dulongensis	Dulongjiang, Yunnan, China*	KIZ035027	MW128102
Odorrana exiliversabilis	Wuyishan, Fujian, China*	HNNU0607032	KF185056
Odorrana fengkaiensis	Shiwanshan, Guangxi, China	HNNU295 7k	KF185033
Odorrana geminata	Cao Bo, Ha Giang, Vietnam	AMNH 163782	EU861546
Odorrana grahami	Kunming, Yunnan, China*	HNNU1008II016	KF185051
Odorrana graminea	Wuzhishan, Hainan, China*	HNNU0606123	KF185038
Odorrana hainanensis	Wuzhishan, Hainan, China*	HNNU0606105	KF185032
Odorrana heatwolei	Phongsaly, Phongsaly, Laos*	FMNH 258134	OR237216
Odorrana heatwolei	Mengla, Yunnan, China	KIZ2019541	OR237217
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194301	OR237218
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194302	OR237219
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194255	OR237220
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194256	OR237221
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194257	OR237222
Odorrana heatwolei	Mengla, Yunnan, China	KIZ20194258	OR237223
"*Odorrana tiannanensis*"	Houey Phihet, Phongsaly, Laos	2005.0180	KR827975
"*Odorrana tiannanensis*"	Houey Phihet, Phongsaly, Laos	2005.0183	KR827976
"*Odorrana tiannanensis*"	Long Nai Khao, Phongsaly, Laos	2004.0406	KR827977
"*Odorrana tiannanensis*"	Long Nai Khao, Phongsaly, Laos	2004.0407	KR827978
"*Odorrana tiannanensis*"	Nathen, Phongsaly, Laos	2004.0408	KR827979
"*Odorrana tiannanensis*"	Houey Phihet, Phongsaly, Laos	2005.0182	KR827980
Odorrana hejiangensis	Hejiang, Sichuan, China*	HNNU1007I202	KF185052
Odorrana hosii	Kuala Lumpur, Malaysia	No voucher	AB511284
Odorrana huanggangensis	Wuyishan, Fujian, China*	HNNU0607001	KF185059
Odorrana ishikawae	Amami Island, Ryukyu, Japan	No voucher	AB511282
Odorrana jingdongensis	Jingdong, Yunan, China*	20070711017	KF185050
Odorrana junlianensis	Junlian, Sichuan, China*	HNNU002	KF185058
Odorrana kuangwuensis	Nanjiang, Sichuan, China*	HNNU0908II185	KF185034
Odorrana kweichowensis	Shilian, Meitan, Guizhou, China	CIBGYU20130917004	MH193548

Species	Locality	Voucher NO.	GenBank NO.
Odorrana leporipes	Shaoguan, Guangdong, China*	HNNU1008I099	KF185036
Odorrana liboensis	Maolan, Libo, Guizhou, China*	GZNU20160802003	MW481352
Odorrana lipuensis	Lipu, Guilin, Guangxi, China*	NHMG1306002	KM388699
Odorrana livida	Thagata Juwa, Myanmar*	BMNH 1889.3.25.48	DQ650615
Odorrana lungshengensis	Longsheng, Guangxi, China*	HNNU70028	KF185054
Odorrana macrotympana	Yingjiang, Yunnan, China*	KIZ 2009051020	OL831010
Odorrana macrotympana	Htamanthi, Sagaing, Myanmar	SEABRI 2019120040	OL831011
Odorrana macrotympana	Htamanthi, Sagaing, Myanmar	SEABRI 2019120041	OL831012
Odorrana macrotympana	Htamanthi, Sagaing, Myanmar	SEABRI 2019120072	OL831013
Odorrana macrotympana	Htamanthi, Sagaing, Myanmar	SEABRI 2019120073	OL831014
Odorrana margaretae	Emei, Sichuan, China	HNNU20050032	KF185035
Odorrana morafkai	Tram Lap, Gia Lai, Vietnam	ROM7446	AF206484
Odorrana mutschmanni	Cao Bang, Vietnam*	IEBR 3725	KU356766
Odorrana nanjiangensis	Nanjiang, Sichuan, China*	HNNU1007I291	KF185042
Odorrana narina	Okinawa Island, Ryukyu, Japan	No voucher	AB511287
Odorrana nasica	Ha Tinh, Vietnam	AMNH A161169	DQ283345
Odorrana nasuta	Wuzhishan, Hainan, China*	HNNU051119	KF185053
Odorrana sangzhiensis	Sangzhi, Hunan, China*	CSUFT 4305220051	MW464865
Odorrana schmackeri	Yichang, Hubei, China*	HNNU0908II349	KF185047
Odorrana supranarina	Iriomotejima, Ryukyu, Japan	KUHE2898	AB200950
Odorrana swinhoana	Nantou, Taiwan, China	HNNUTW9	KF185046
Odorrana tianmuii	Tianmushan, Zhejiang, China*	NHMG1303018	KT315390
Odorrana tiannanensis	Hekou, Yunnan, China*	SCUM50510CHX	EF453751
Odorrana tiannanensis	Hekou, Yunnan, China*	KIZ20193272	OL831009
Odorrana tiannanensis	Hekou, Yunnan, China*	KIZ20193273	OL831008
Odorrana tiannanensis	Hekou, Yunnan, China*	KIZ20193274	OL831007
Odorrana tiannanensis	Hekou, Yunnan, China*	KIZ20215191	OL831006
Odorrana tiannanensis	Gejiu, Yunnan, China	KIZ20193241	OR237224
Odorrana tiannanensis	Gejiu, Yunnan, China	KIZ20193242	OR237225
Odorrana tiannanensis	Gejiu, Yunnan, China	KIZ2020411	OR237226
Odorrana tiannanensis	Malipo, Yunnan, China	KIZ20215121	OR237227
Odorrana tiannanensis	Malipo, Yunnan, China	KIZ20215122	OR237228
Odorrana tiannanensis	Malipo, Yunnan, China	KIZ20215123	OR237229
Odorrana tiannanensis	Malipo, Yunnan, China	KIZ20215124	OR237230
Odorrana tormota	Huangshan, Anhui, China*	No voucher	DQ835616
Odorrana trankieni	Vietnam	VNMN04035	KX893900
Odorrana utsunomiyaorum	Iriomotejima, Ryukyu, Japan	KUHE12896	AB200952
Odorrana versabilis	Leishan, Guizhou, China*	HNNU003 LS	KF185055
Odorrana wuchuanensis	Wuchuan, Guizhou, China*	HNNU019 L	KF185043
Odorrana yentuensis	Vietnam	IEBRA.2015.38	KX893891
Odorrana yizhangensis	Yizhang, Hunan, China*	HNNU1008I075	KF185048
Odorrana yunnanensis	Longchuan, Yunnan, China*	HNNU001YN	KF185057
Pelophylax nigromaculatus	Locality unknown	No voucher	LC389208
Rana chensinensis	Ningshan, Shanxi, China	HNNU20060359	KF185061

SVL 37.1–57.3 mm in adult males, 97.3–106.7 mm in adult females; head length slightly greater than head width; dorsal skin shagreened, skin on flanks granular; supratympanic fold present; dorsolateral folds distinct in males and indistinct in females; tympanum large in males (TD/ED 0.58–0.73) and relatively small in females (TD/ED 0.45–0.58); vomerine teeth distinct; relative lengths of fingers III > IV > I > II; inner metacarpal tubercle and outer metacarpal tubercle present, outer metatarsal tubercle absent; all finger and toe tips slightly expanded; toes with entire webbing to disks; uniform light brown or dark brown on whole body, dense tiny black dots scattered on dorsum; paired external vocal sacs and nuptial pad on the base of finger I present in adult males.

Specimens examined. KIZ20194255, adult male, and KIZ20194256–KIZ20194258, three adult females, collected on 24 April 2019 from Mandan village, Mengla Town, Mengla County, Xishuangbanna Prefecture, Yunnan Province, China (21°28'59"N, 101°40'29"E, 780 m elevation) by Shuo Liu; KIZ20194279, adult female, collected on 27 April 2019 from Mengyuan village, Guanlei Town,

Table 2. Genetic divergences (uncorrected p-distance, %) based on the mitochondrial 16S rRNA gene sequences.

	1	2	3	4
1 *Odorrana heatwolei* (Holotype)				
2 *Odorrana heatwolei* (Mengla, China)	0.20			
3 "*Odorrana tiannanensis*" (Phongsaly, Laos)	0.28	0.17		
4 *Odorrana tiannanensis*	6.47	6.51	3.75	
5 *Odorrana macrotympana*	10.10	10.25	10.78	9.70

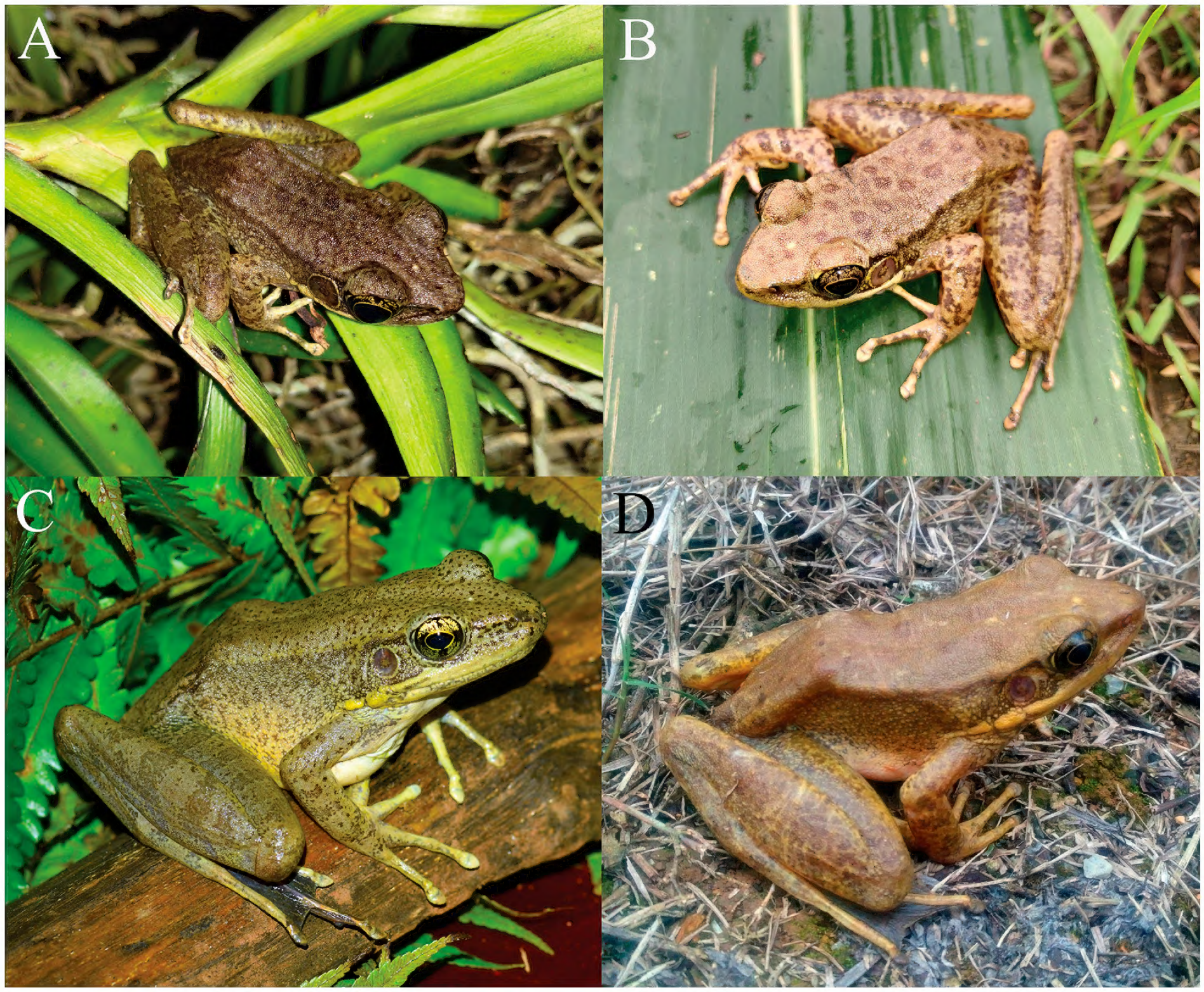

Figure 3. Comparison between *Odorrana heatwolei* and *O. tiannanensis* in life. **A.** Adult male *O. heatwolei* from Mengla, Yunnan, China; **B.** Adult male *O. tiannanensis* from Hekou, Yunnan, China; **C.** Adult female *O. heatwolei* from Mengla, Yunnan, China; **D.** Adult female *O. tiannanensis* from Hekou, Yunnan, China.

Mengla County, Xishuangbanna Prefecture, Yunnan Province, China (21°38'35"N, 101°26'54"E, 950 m elevation) by Shuo Liu; KIZ20194301–KIZ20194302, two adult males, collected on 30 April 2019 from Bubeng village, Mengla Town, Mengla County, Xishuangbanna Prefecture, Yunnan Province, China (21°36'21"N, 101°33'27"E, 800 m elevation) by Shuo Liu; KIZ2019541, adult male, and KIZ2019542, adult female, collected on 4 May 2019 from Xinshan village, Yaoqu Township, Mengla County, Xishuangbanna Prefecture, Yunnan Province, China (21°54'59"N, 101°32'16"E, 840 m elevation) by Shuo Liu.

Description of the specimens from China. Morphometric and meristic data are presented in Table 3. SVL 46.8–51.7 mm in males, 97.4–106.7 mm in females; head width slightly shorter than length (HW/HL 0.87–0.91 in males, 0.93–0.98 in females); snout obtuse, pointed in dorsal view and rounded in profile, obviously projecting beyond lower jaw; nostril closer to snout than to eye; canthus rostralis distinct; loreal region concave; internarial distance greater than interorbital distance; snout length greater than eye diameter; pineal body distinct; supratympanic fold horizontal and straight; tympanum large in males (TD/ED 0.66–0.73) and relatively small in females (TD/ED 0.48–0.58), round and transparent; vomerine teeth developed into mass on two oblique ridges between the two choanae; tongue cordiform, posterior notch enlarged and formed as U-shaped; vocal sac openings on floor of mouth in each corner and an external vocal sac behind each angle of mouth in males.

Forelimbs robust; relative lengths of fingers III > IV > I > II; all finger tips slightly expanded; lateral fringes and webbing on fingers absent; subarticular tubercle round and prominent; one oval thenar tubercle prominent on the ventral of finger I; inner metacarpal tubercle and outer metacarpal tubercle distinct; supernumerary tubercles at the base of fingers II–IV; grayish-yellow nuptial pad on finger I in adult males.

Hind limbs long, tibia longer than thigh; toes long, relative lengths IV > V > III > II > I; all toe tips slightly expanded; toes with entire webbing to disks; subarticu-

Figure 4. Dorsal view (**A**), lateral view (**B**), and ventral view (**C**) of the male (KIZ20194255) and dorsal view (**D**), lateral view (**E**), and ventral view (**F**) of an adult female (escaped) of *Odorrana heatwolei* from China in life.

lar tubercles prominent and longitudinally ovoid; inner metatarsal tubercle prominent and oval; outer metatarsal and supernumerary tubercles absent.

Dorsal skin shagreened with some very indistinct tubercles, skin on flanks granular, ventral skin smooth, and dorsolateral folds distinct in males. Skin slightly smoother and dorsolateral folds more indistinct in females.

Coloration in life. Dorsum brown scattered with dense tiny brownish black dots; upper lip yellowish white with indistinct dark spots; lower lip creamy white with distinct dark spots; lateral side of head and body brown with many irregular dark brown spots; dorsal surfaces of limbs brown with some indistinct dark brown bands; ventral surface of head and forelimbs, chest, and belly

Table 3. Morphological measurements (mm) of the specimens of *Odorrana heatwolei* from China.

	KIZ2019541	KIZ20194301	KIZ20194302	KIZ20194255	KIZ20194256	KIZ20194257	KIZ20194258	KIZ20194279	KIZ2019542
	Male	Male	Male	Male	Female	Female	Female	Female	Female
SVL	51.7	48.3	48.8	46.8	97.4	102.7	103.4	106.7	104.2
HL	21.8	20.3	19.6	19.7	37.5	37.7	37.4	39.2	39.0
HW	19.1	17.7	17.9	17.2	34.9	36.1	35.7	36.9	38.4
SL	8.9	8.8	8.3	8.5	16.4	15.7	16.3	16.4	16.6
IND	5.4	5.8	5.3	5.5	10.3	10.0	9.8	10.4	11.0
IOD	4.2	4.1	4.0	4.6	8.7	9.4	8.1	9.6	9.5
ED	7.2	7.6	7.1	7.0	10.5	11.0	10.9	12.2	11.1
UEW	5.2	5.1	4.8	4.8	7.5	7.7	7.6	7.7	8.4
TD	5.2	5.3	4.7	5.1	6.1	5.9	6.0	5.8	5.7
TED	1.7	1.5	1.5	1.6	4.5	4.4	4.7	5.0	4.8
FHL	28.2	25.7	26.4	26.3	49.1	51.2	50.3	53.0	55.1
HAL	16.0	15.1	15.3	15.6	28.6	30.1	29.6	31.4	31.9
TL	34.3	31.5	32.9	31.2	65.6	66.5	65.9	70.4	71.8
TFL	44.1	40.3	42.0	40.6	83.2	86.0	82.6	90.6	94.1
FTL	29.5	27.3	28.4	26.9	55.7	59.0	56.5	60.7	65.0
FDW3	1.9	1.9	1.8	1.8	3.7	3.5	2.6	3.6	4.0

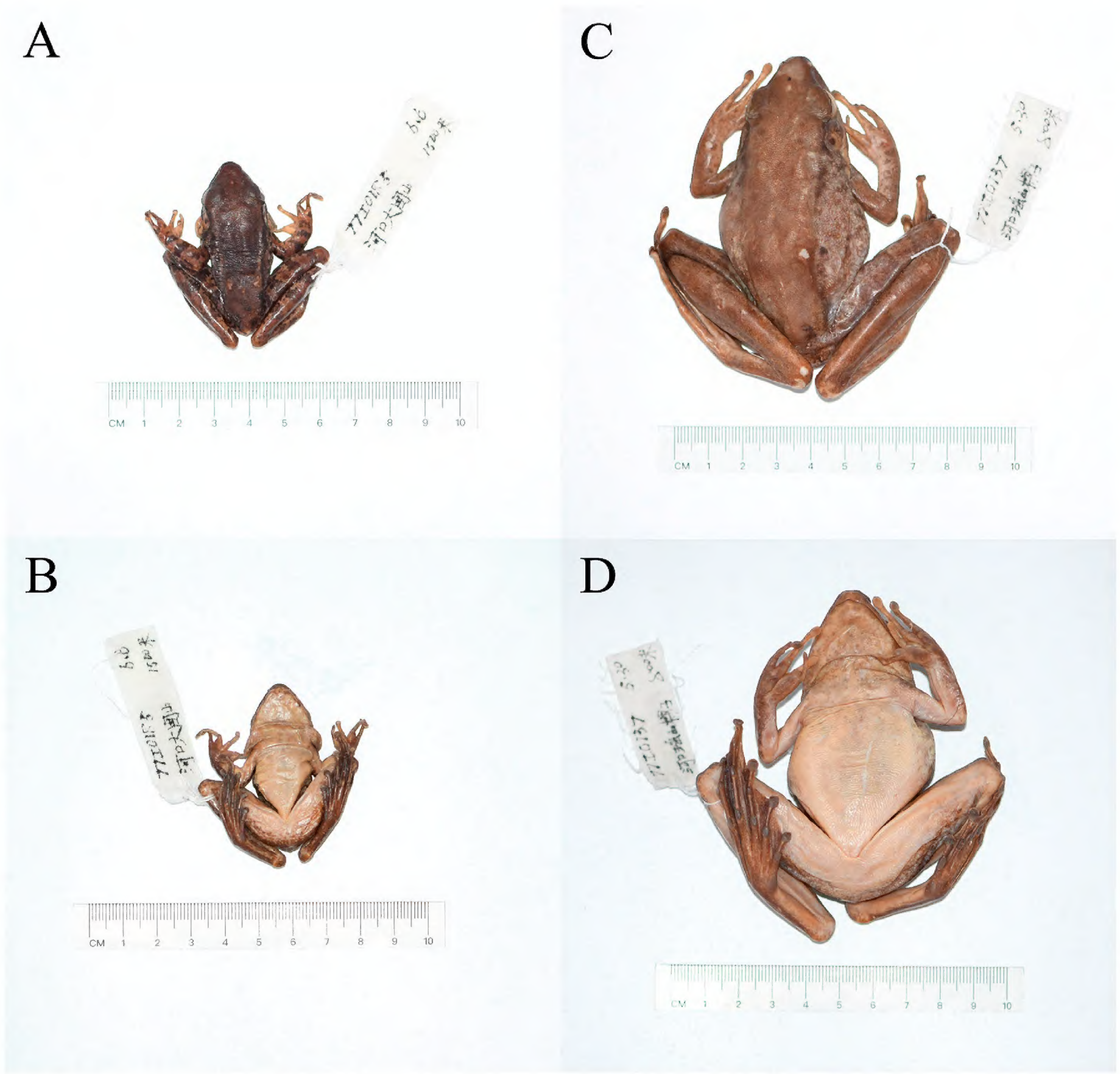

Figure 5. The type specimens of *Odorrana tiannanensis* in preservative. **A.** Dorsal; **B.** Ventral views of the holotype (KIZ 77I0185, male); **C.** Dorsal; **D.** Ventral views of the allotype (KIZ 77I0137, female).

Figure 6. Dorsal view (**A**) and ventral view (**B**) of the specimens of *Odorrana heatwolei* from China in preservative.

creamy white; ventral surface of hindlimbs light yellow; buttocks slightly pink; tympanum dark brown; and iris yellow in males. Coloration in females very similar to but usually slightly lighter than that in males.

Coloration in preservative. Dorsum color turned darker to grayish black, the dense tiny black dots on dorsum still visible, dorsal color of limbs turned darker to brownish black, the bands on limbs became indistinct. Ventral color of head and forelimbs, chest, and belly faded to pale white, ventral color of hindlimbs turned to flesh color. Iris became black, pupil became white.

Natural history. The specimens from China were all found on the banks of rivers at night. No eggs or tadpoles were found from April to May. There were many stones and forests with good vegetation on the banks of the river (Fig. 8). An *Amolops* species of *Amolops* cf. *vitreus* (Bain, Stuart & Orlov, 2006) is distributed sympatric with this species.

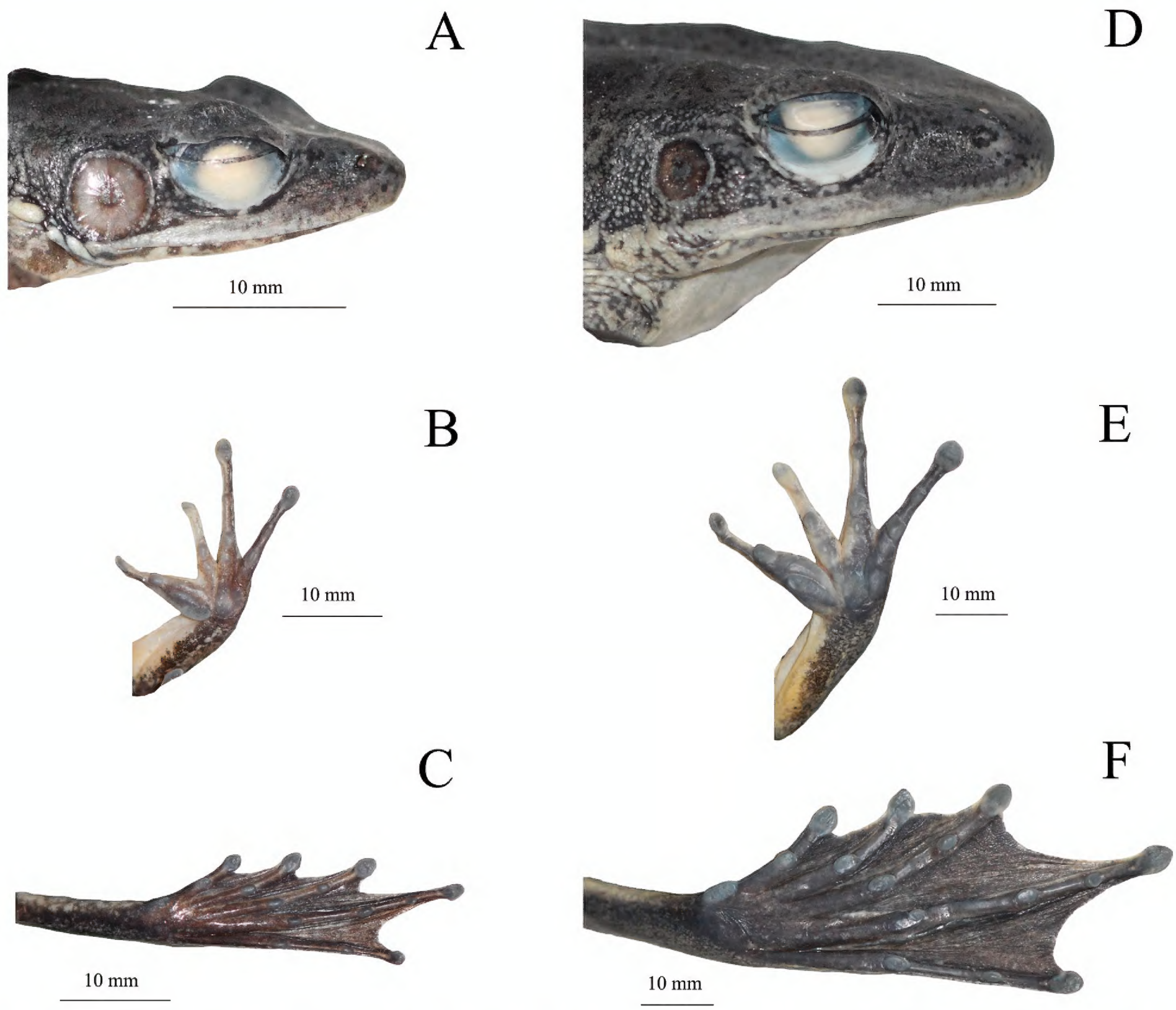

Figure 7. Close-up views of the head (**A**), vola (**B**), and planta (**C**) of the male (KIZ2019541) and close-up views of the head (**D**), vola (**E**), and planta (**F**) of the female (KIZ2019542) of *Odorrana heatwolei* from China in preservative.

Figure 8. The habitat at the collection site of the specimens of *Odorrana heatwolei* in Mengla, Yunnan, China.

Distribution. Currently known in Phongsaly Province, Laos, and Xishuangbanna Prefecture, Yunnan Province, China (Fig. 1).

Discussion

Ohler (2007) took *Odorrana heatwolei* as a synonym of *O. tiannanensis* based on only morphological characteristics. These two species are indeed very similar in morphological measurements, but their body colorations are significantly different. In addition, these two species form two separate lineages molecularly and the genetic distance between them is large.

The straight distance between the type locality of *Odorrana heatwolei* and the type locality of *O. tiannanensis* is approximately 200 km, and they are separated by the Red River (Song Hong River in Vietnam). The straight distance between the collection site of the specimens of *O. heatwolei* from Xishuangbanna, Yunnan, China, and the type locality of *O. heatwolei* is approximately 60 km, and there is no obvious geographical obstacle between them. These specimens from Xishuangbanna are the first record of *O. heatwolei* from China.

Odorrana tiannanensis was considered previously to be widely distributed in southern Yunnan, China, and northern Vietnam and northern Laos (Frost 2023). We found that this species is likely to be distributed only in the east of the Red River including southeastern Yunnan, China, and northeastern Vietnam, and *O. heatwolei* is likely to be distributed only in the west of the Red River including south-central and southwestern Yunnan, China, and northern Laos. More samples are needed to verify the geographical isolation between the two species.

It was found previously that *Odorrana macrotympana* and *O. tiannanensis* are closely related (Liu et al. 2022), however, the distributions of these two species are far apart, one in westernmost Yunnan and northern Myanmar, and the other one in southeastern Yunnan (Fig. 1), and no other species was found that can connect these two species in the large area between their distributions, which seems unlikely. *Odorrana heatwolei* just filled this gap. However, the distribution of *O. heatwolei* is close to that of *O. tiannanensis* and far apart from that of *O. macrotympana*. Therefore, we speculate that there may be species that can connect *O. heatwolei* and *O. macrotympana* in the area between their distributions. More investigations in these areas are needed to verify this speculation.

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